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## SOME NEW VARIETIES OF RATS AND GUINEA-PIGS AND THEIR RELATION TO PROBLEMS OF COLOR INHERITANCE

PROFESSOR W. E. CASTLE

HARVARD UNIVERSITY

THE marvelous color variation of the domesticated animals has been recognized as a capital illustration of evolution from the time of Darwin to the present, and much study has been devoted to the question of how it has taken place. Nevertheless we have very little positive information as to how existing color varieties originated, and theories differ concerning the matter.

It becomes therefore important to record carefully any contemporary events which may throw light on the subject. This is my excuse for calling the attention of scientists to the recent appearance in England of two new and striking color variations of the common or Norway rat. I say "appearance" advisedly for it is impossible to say how long these variations may have been in existence within the race, cropping out perhaps from time to time sporadically. Certain it is, however, that they have only quite recently come to the attention of "fanciers," who have taken them up with great enthusiasm.

The new varieties are known to the fancy as (1) *pink-eyed* yellow, fawn, or cream; and (2) *black-eyed* yellow, fawn, or cream. From the evidence at hand it is clear that each of the two variations has originated *in the wild*

race and as a mutation or unit-character variation, *retrogressive* in nature (*i. e.*, due to loss of some normal constituent from the germplasm). Each is a simple Mendelian recessive character in crosses with wild race, and with certain at least of the tame varieties. The two variations have not as yet been combined by intercrossing, but this will be attempted soon and, I doubt not, with entire success.

My first information about the new variations was obtained from *Fur and Feather*, the official organ of the English fanciers, in which appeared advertisements of "the new variety" of black-eyed yellow rat. Now as long ago as 1903 Bateson had commented on the singular absence of a "yellow" variety among rats, noteworthy because nearly all mammals kept in captivity have such varieties; and I have since been bold enough to publish some speculations as to why this variation had not made its appearance. Consequently I was much excited to learn that it actually had appeared. Miss M. Douglas, one of the editors of *Fur and Feather*, and secretary of the National Mouse and Rat Club (of England) very kindly answered my inquiries about the new varieties and put me in communication with the "originators," who have given so clear and full accounts of their procedure in establishing the new varieties that even the genetic behavior of the variations is fairly certain, though I purpose to confirm this fully with experiments which are already in progress.

The pink-eyed variation made its appearance first, so far as known, about 1910 or 1911, but it had probably been in existence for some time and become rather widely diffused throughout the central part of England, for at about the same time pink-eyed wild rats were caught at or near Preston and at Chesterfield, cities some 65 miles apart. I am informed that Mr. T. Robinson at Preston and Mr. W. E. Marriott at Chesterfield independently established the "pink-eyed fawn" variety, or what would better be called the *pink-eyed agouti* variety, since appar-

ently it differs from the wild gray (or agouti) variety by the pink-eyed variation alone. It is not a true *yellow* variety at all genetically, though (like the pink-eyed gray mouse) it resembles one superficially because of the yellow ticking of the agouti fur.

It is also quite distinct genetically from the *albino* variation seen in white rats, yet its "dirty white" color is enough like the appearance of the albino to permit mistaking one for the other. Possibly this is why the pink-eyed variation may have been for some time overlooked.

Mr. Robinson has not answered my inquiries, but Mr. Mariott writes in detail about his observations and experiments.

Under date of October 11, 1913, he says:

The first rat with any semblance of fawn in it that I had was caught in a trap on a provision merchant's premises in Chesterfield. You could scarcely call it a fawn, but more of a cream or dirty white. I have also had four others similar to this one, 2 caught at the same place and 2 caught at a malt-house in close proximity to the other premises, [in all] 3 bucks and 2 does, but the only one that I was able to get to breed was the first brought to me, which was a buck. When first caught it was very wild, in fact it appeared to me to be more wild than an ordinary wild rat. It was a source of trouble getting it to mate, killing no less than 20 does before mating. I eventually got it mated to 2 does, one a pure white for at least 10 generations, and one black-and-white hooded-and-striped, or Japanese rat. The result of the pure white cross was 2 young, a buck and a doe, *which were agoutis with no white at all*.<sup>1</sup> The result from the Japanese cross was 7 young, 5 does and 2 bucks, which were the color of Irish agoutis being agouti color with a white stripe running underneath. These results naturally caused me great disappointment as I was expecting a fawn colored young one. When the young were old enough I mated father and daughter, result *nil*; mother and son, result *nil*; brother and sister. The brother and sister mating from the pure white cross produced 2 fawn colored rats, a buck and a doe, and 5 agoutis.<sup>2</sup> The brother and sister mating from the Japanese cross produced 2 fawn-and-white Japanese, 1 cream-and-white Japanese,

<sup>1</sup> Italics mine. Note the reversion to full wild color. This shows the pink-eyed variation to be entirely different in nature from the ordinary albino variation.

<sup>2</sup> Note the return of "fawn" (pink-eyed agouti) as a recessive character in approximately 1 in 4 young.

1 black-and-white Japanese, and 4 agoutis.<sup>3</sup> The fawns and fawn-and-whites resulting from these crosses were much deeper in color than the wild grandsire. Mated one with another they gave a proportion of about 2 fawn colored or fawn-and-white in 7 young.<sup>4</sup> I may say in conclusion that the original wild rat was in shape of body, skull, etc., as the ordinary brown or agouti rat that we have running wild in this district.

Mr. Marriott sold a "fawn-and-white" (pink-eyed hooded agouti) buck to Mr. E. F. Tilling, of Hessenford, who also "originated" the second variation, the "black-eyed yellow," or true yellow variation. His results from the pink-eyed variation confirm those of Mr. Marriott.

Mr. Tilling writes under date of October 18, 1913:

I see by *Fur and Feather* this week that you are interested in the yellow and cream varieties of rats. I am also much interested in these and have produced the latter variety within the last few months. We have 2 kinds over here, the yellow-and-white hooded with pink eyes and the self yellow (and cream) with black eyes. Both are quite distinct. The first mentioned was produced some 2 or 3 years ago. Mr. Marriott, of Chesterfield, bred the first I heard of from a wild caught fawn. He bred a couple of yellow and white hooded bucks of which Miss Douglas bought one and I the other. I mated mine to about 15 does of various colors and definite strains. He was a splendid breeder and got some very fine youngsters, but *not one of his own color from the first cross*.<sup>5</sup> I subsequently mated him to some of his daughters and they produced a good proportion of yellow-and-white young.<sup>6</sup> These are now fairly plentiful over here and are in the hands of several fanciers.

Of the other kinds, black-eyed fawns and creams, the first one exhibited and from which all mine are descended, was a very fine wild caught, deep colored, fawn specimen. I got her partly tame and exhibited her at the National Mouse and Rat Club's annual show at Bristol on November 27 and 28, 1912, where she won first in the self class and

<sup>3</sup> "Fawn- and white Japanese" means (to me) pink-eyed agouti with the "Japanese" color pattern (hooded). The formation of this class of young shows the hooded pattern ("Japanese") to be independent in transmission of the pink-eyed variation. "Cream-and-white Japanese," I interpret as pink-eyed *black* (non-agouti) hooded. "Black-and-white Japanese" is the familiar black hooded. We should expect this mating to produce also *self* pink-eyed agouti and *self* pink-eyed black which are not mentioned.

<sup>4</sup> The Mendelian expectation is 2 in 8.

<sup>5</sup> Italics mine. Note again the recessive nature of the variation.

<sup>6</sup> Not real yellow-and-white, as already explained, but pink-eyed agouti-and-white or black-and-white.

was well commented upon in the fanciers' papers. From this doe I have built up my strain of black-eyed creams. I mated her to a self black buck and she bred 8 youngsters all wild colored.<sup>7</sup> This is the only litter I had from her, as shortly afterward, during my illness, my man while transferring her from one cage to another let her get away and was unable to recapture her. However, I have bred from her youngsters, mating brother and sister, and the litters have invariably contained at least 1 fawn or cream<sup>8</sup> each time. I have now just bred for the first time from the 3 first does so produced, again mating them to their brother and the result is litters of 7, 5 and 7, respectively, all self creams.<sup>9</sup>

From the statements of Messrs. Marriott and Tilling, it is evident that the two variations, which they, respectively, have introduced into the rat fancy, are both recessive in heredity, as are also the three previously known Mendelizing color variations of rats, viz., (1) the albino variation (with uncolored coat and eyes); (2) the black variation (lacking the agouti ticking of the fur); and (3) the piebald "hooded" pattern of white and colored fur. Each of these is known to be an independent Mendelizing unit-character. If the new variations are as supposed independent of each other and of those previously known, they will make possible the immediate four-fold increase in number of the previously known color varieties of rats. If for the present we adopt a simplified terminology (as I have elsewhere suggested) for the different color variations, employing small letters for such as are recessive in heredity, we may use the following set of symbols:

|                |              |
|----------------|--------------|
| White (albino) | = <i>w</i> , |
| Black          | = <i>b</i> , |
| Hooded         | = <i>h</i> , |
| Pink-eyed      | = <i>p</i> , |
| Yellow         | = <i>y</i> , |

<sup>7</sup> This shows that the original yellow animal was potentially an *agouti*. A pair of yellows which Mr. Tilling has sent me have *light bellies* and I presume are also potentially agoutis.

<sup>8</sup> "Cream" here probably means yellow not transmitting agouti. It probably lacks the lighter belly as do yellow rabbits which do not transmit agouti.

<sup>9</sup> This shows that extracted yellows breed true to yellow. Hence the variation is recessive, as in rabbits and guinea-pigs, not dominant as in mice.

By various combinations of these variations, if each is independent of all the others, 32 varieties become possible. Half of these varieties will be albinos, white and so visibly indistinguishable. The other 16, we have reason to suppose, will look different from each other. Previously we had but four of these, the first four in the following list of the theoretically possible 16.

1. *Normal or wild* ..... *agouti*.
2. *b* ..... *black*,
3. *h* ..... *hooded*,
4. *bh* ..... *black hooded*,
5. *p* ..... *pink-eyed*,
6. *pb* ..... *pink-eyed black*,
7. *ph* ..... *pink-eyed hooded*,
8. *pbh* ..... *pink-eyed black hooded*,
9. *y* ..... *yellow*,
10. *yb* ..... *yellow black (i. e., non agouti yellow)*,
11. *yh* ..... *yellow hooded*,
12. *yp* ..... *yellow pink-eyed*,
13. *ybh* ..... *yellow black hooded*,
14. *yph* ..... *yellow pink-eyed hooded*,
15. *yph* ..... *yellow pink-eyed hooded*,
16. *yph* ..... *yellow pink-eyed black hooded*.

Varieties 1-4 have been known for some time; they have constituted the fancier's entire repertoire up to the present time. Varieties 5 and 9 have apparently arisen as wild sports obtained by Marriott and Tilling, respectively. By crosses these gentlemen have apparently obtained varieties 6, 7, 8, and probably 10. Varieties 11-16 are as yet unknown, but will doubtless soon be produced. Corresponding with each of the 16 colored varieties, an uncolored one should be possible of production, which would transmit in crosses with any colored variety the characteristics indicated by its formula. Albinos corresponding to colored varieties 1-4 are positively known to occur; their symbols would be *w*, *wb*, *wh* and *wbh*, respectively. Symbols for the remaining 12 expected varieties may be formed in like fashion, by prefixing *w* to the combinations already given.

All the five unit-character variations, which in different combinations are responsible for the color varieties of

rats, have their parallels in other mammals. Albinism and white-spotting (which in rats takes the form of the hooded pattern) are among the commonest. They occur in practically all mammals from mice to men. Albinism appears to consist in such a modification of metabolism that the process of pigment-formation can take place only feebly or not at all. That particular process which seems chiefly affected is the production of yellow pigment. Albinos, so far as I know, never produce genuine yellow pigment, though they may produce considerable quantities of black or brown pigment, as in the case of the Himalayan rabbit. An undescribed variety of guinea-pig, which I obtained about two years ago in Peru, may bear as much *black* pigment in its coat as wild cavies do, yet it forms no yellow pigment at all. Further this variation behaves as the allelomorph of ordinary albinism, indicating that it is probably of the same genetic character. For this reason *we may provisionally consider the albinism of mammals as due to a loss of the ability to form yellow pigment.* This usually, if not always, involves a lessened capacity to form other pigments also, so that it seems probable that the same chemical process, which produces yellow pigment as an end-product, is ordinarily involved also in producing the higher oxidation stages seen in brown and black pigment. In albinos this process would seem to be omitted, or to be accomplished by some step which does not involve the production of yellow pigment.

The yellow variation is extremely common in mammals. Yellow varieties, which at opposite extremes of intensity of pigmentation are known as *cream* and *red*, occur among horses, cattle, hogs, cats, dogs, rabbits, guinea-pigs, mice and human beings. In this variation pigment oxidation stops at the yellow stage, usually throughout the coat but not in the eye. Described in negative terms a yellow variety is one in which black and brown are suppressed or restricted. Black and brown, though usually restricted to the *eye* in yellow varieties, may occur also in



small quantities in the fur. Examples are found among horses (bay and dun varieties), cattle (the Jersey breed), dogs (the common dirty yellow variety), rabbits (the "tortoise-shell" variety), mice and guinea-pigs, and probably red-haired human beings also.

Black varieties of mammals arise in two genetically distinct ways. One is a quantitative increase or extension of black, the reverse of what happens in yellow varieties, so that black encroaches on regions normally yellow or may even obliterate them altogether. Examples are found in black squirrels, in which the agouti yellow ticking of the fur is almost, but not quite, obliterated by black pigment. But the "black" variation of rats, mice, guinea-pigs and ordinary rabbits results from a total loss, not a covering up, of the yellow ticking of the fur seen in agouti varieties. Genetically it is quite distinct from the other kind of black. It is a recessive variation and so breeds true.

The *pink-eyed* variation is the rarest of all the five enumerated as occurring in rats. It has been known heretofore only in mice, though I have recently obtained it also in guinea-pigs from Peru, where it seems to be well established.

In this variation the capacity to form yellow pigment is unimpaired, but only *traces* of black or brown pigment are produced. Consequently varieties which possess the other genetic factors of normal yellow animals have fully pigmented (yellow) fur, but with very faintly pigmented (pink) eyes, when they possess this factor. If, however, they possess the other genetic factors of black, brown, or agouti varieties, along with this pink-eyed variation, then both the fur and the eyes are very faintly pigmented. From this results the seeming paradox that pink-eyed blacks are less heavily pigmented than pink-eyed yellows, so that in rats the fanciers have called the former "creams," the latter "fawns."

When pink-eyed animals are crossed with albinos, offspring fully colored (eyes and all) result, as was first

shown by Darbishire some ten years ago. This indicates that the two variations are not only genetically distinct, but are physiologically complementary. The albino has defective metabolism for producing yellow (and in consequence brown and black also); the pink-eyed animal has the full mechanism for forming yellow, but its brown and black producing mechanism is defective. Together they possess the full mechanism of normal color production. Hence the reversion on crossing.

White spotting is clearly due to neither of the above modifications, but to a different change in the metabolism so that no pigment at all is produced. For an albino rabbit or guinea-pig may, as already observed, bear considerable black or brown pigment, but a white spot either on an albino, on a pink-eyed animal, or on a fully colored animal is entirely devoid of pigment. The paradox of a white spot on an albino is obtainable by crossing a white-spotted colored race with an albino race, which develops some pigment in the fur, as for example the Himalayan race of rabbits and guinea-pigs. In this way English-marked Himalayan rabbits and spotted albino guinea-pigs have been produced in my laboratory.

*Postscript:* While this paper was in press, Mr. Tilling, in reply to a further inquiry, wrote that his original black-eyed yellow rat was caught on a ship at Liverpool. The fact that the pink-eyed variety was found in the same general region leads him to believe that both variations were introduced on ships from some foreign country. It would be of much interest to know from what country or countries. Any information on this point obtainable from rat-catchers or others would be welcome.